

larger-sized (45–49 μm) walnut pollen grains in the historic-age sediments of the Roberts Island core may be derived from *Juglans regia* L. growing in orchards adjacent to the Delta (unpubl. data; Stone and Broome, *In*: Nilsson, ed., World pollen spore fl. 4. 1975).

In all instances *Juglans* pollen is well preserved and does not appear to be redeposited from earlier sediments in the Sacramento-San Joaquin drainage systems. Accordingly, I believe that the *Juglans* is in primary deposits derived from trees growing within the drainage system over the last 5000 years.

Thompson's suggestion regarding the presence of walnut pollen in the Delta deposits is correct. Although the available pollen record does not preclude the dispersal of walnut in central California by prehistoric human activity, it does indicate that the trees were present in the Delta thousands of years prior to the earliest known Euro-American entry into the area.—G. JAMES WEST, Department of Anthropology, University of California, Davis 95616. (Received 2 Nov 1979; revision received and accepted 26 Sep 1980.)

AGES OF INVASIVE TREES IN DANA MEADOWS, YOSEMITE NATIONAL PARK, CALIFORNIA.—Throughout the high elevations of the Sierra Nevada, meadows are commonly invaded by lodgepole pine (*Pinus contorta*). In 1978, I investigated the age structure of trees in Dana Meadows, about 2 km south of the Tioga Pass entrance station to Yosemite National Park. These meadows are bordered by monotypic stands of lodgepole pine. On both the north and south sides of the meadow, five belt transects 2 m wide were located 30 m apart. Each of the ten transects was extended perpendicularly from the forest-meadow ecotone into the meadow to the most distant tree encountered; transect lengths varied from 10.4 m to 100 m. The largest number of trees in a transect was 32, and the smallest was 5. An eleventh sample, a quadrat 10 m by 2 m and containing 23 trees, was established within the meadow in an area of dense young trees. All trees rooted within the sample areas were cored at their bases with an increment borer; ages were estimated to be the number of rings on the cores plus 2. Trees too small to core were cut at their bases and the rings counted on the stumps. In addition to the trees within the samples, the four largest trees well within the meadow, which occurred in a stand of 12 individuals, were cored. In total, the ages of 149 trees were determined; these were aggregated into five-year age-classes for analysis.

Invasion by large numbers of trees apparently began about 1925, although all five-year periods between 1910 and 1975 were represented by trees; a few trees germinated and survived within the meadow in still earlier years (Table 1). The oldest tree within the transects germinated about 1866 (other germination dates for trees in this stand: 1887, 1902, 1910). In general, the older trees appeared healthy, but 40 percent of the trees established after 1950 had dead leaders. In addition, 16 dead trees were encountered in the 11 sample areas; judging by size-age correlations, none of these was older than 30 years when it died.

The distribution of trees of certain conditions and ages along the transects produced only weak patterns. The dead trees were not restricted to particular locations along the transects, but most of the trees with dead tops were not immediately adjacent to the forest edge. The correlation between position on the transects and age was not significant ($r^2 = 0.08$), although trees encountered in the outermost segment of the transects were often younger than those closer to the forest, and the oldest trees within each transect usually tended to be closer to the forest edge than to the end of the transect in the meadow. These patterns suggest that invasion into open meadow by a few individuals is followed by subsequent germination and survival of other trees.

The invasion date of 1925 is more recent than the dates of initial tree establishment reported by either Boche (Factors affecting meadow-forest borders in Yosemite National Park, California. M.S. thesis, U.C.L.A. 1974) for meadows in the lodgepole forests of Yosemite (1898–1909), or Vankat and Major (J. Biogeogr. 5:377–402. 1978) for meadows in the lodgepole forests of the southern Sierra (1910). In his review of three other

TABLE 1. SPRING TEMPERATURE DEVIATIONS, ANNUAL PRECIPITATION, AND NUMBERS OF TREES GERMINATING IN FIVE-YEAR PERIODS FROM 1865. Spring temperatures are deviations of five-year means from the mean monthly temperatures for March, April, and May. Precipitation values are percents of the mean for the period covered. Climatic data are from NOAA for Yosemite Valley.

Period	Spring temp. (°C)	Annual precip.	No. of trees germinating
1865-			1
1870-			0
1875-			0
1880-			0
1885-			1
1890-			0
1895-			1
1900-			2
1905-		122	0
1910-		93	3
1915-	+0.5	84	2
1920-	-2.2	87	3
1925-	+0.7	89	12
1930-	+0.8	76	13
1935-	-0.1	119	14
1940-	+0.3	116	12
1945-	+0.1	95	5
1950-	+0.2	104	12
1955-	+0.1	105	23
1960-	-0.6	99	14
1965-	+0.2	120	18
1970-	+0.4	105	13
1975-	-0.5	83	0

studies of such tree invasions in the southern Sierra Nevada, Wood (Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. Ph.D. dissertation, Calif. Inst. Tech. 1975) found that the initial establishment dates of meadow trees were reported as 1903, 1906, and 1924. Part of the disparity in dates probably reflects site-specific differences in environmental or historical factors, but it may also result from different criteria for identifying the "beginning" of tree invasions. If 1910 is recognized as the date of initial invasion in Dana Meadows, for example, the data presented here become more consistent with other studies.

The identification of the date when the tree invasion "began" becomes especially significant when trying to correlate it with events that may have caused the unstable ecotone. Regardless of which dates are used, climatic fluctuation seems an unlikely trigger for the recent establishment of meadow trees in Dana Meadows or elsewhere in the Sierra Nevada. Warm dry weather has been suggested as a cause of tree invasion in Sierran meadows because such weather desiccates competing herbaceous vegetation and reduces suffocating soil moisture (Boche, *op. cit.*; Wood, *op. cit.*). Franklin and Dyrness (U.S. For. Serv. Gen. Tech. Rept. PNW-8. 1973) found convincing the association between warm dry weather and a period of tree establishment in subalpine meadows in the Pacific Northwest. These warm dry periods early in this century, however, were apparently not unprecedented in the recent past in the Sierra Nevada; particularly noteworthy is the warm dry episode in the mid 1800's (Fritts, *Monthly Weather Rev.* 93:421-443. 1965; Bradley, *Monthly Weather Rev.* 104:501-512. 1976), a relatively recent period with weather presumably favorable for tree invasion when

trees did not become established in Dana Meadows or other subalpine meadows in the Sierra Nevada. The relatively cold dry conditions since 1975 may have contributed to both the lack of recent tree establishment and the high proportion of die-back among small trees. As a period, however, the years of massive tree invasion were not characterized by consistent and distinctive climatic conditions (Table 1).

Other possible causes are environmental changes involving people. Suppression of frequent fires is sometimes considered responsible for these invasions, although the only empirical study of this agency in a Sierran lodgepole forest focuses on a wet meadow and not a dry-mesic meadow such as Dana Meadows (DeBenedetti and Parsons, *J. Forest* (Washington) 77:477-479. 1979). The model of Vankat and Major, which suggests a lag of a decade between the cessation of sheep grazing and the establishment of meadow trees, seems not to fit the data in this study; sheep were not eliminated from Dana Meadows until 1905, decades following the germination of the oldest tree (1866) and far predating the beginning of massive invasion (1925). Yet, their model fits the data better if the date of 1910 is used as the beginning of the invasion; such an interpretation would then also conform more closely with that of Dunwiddie (*Arctic and Alpine Res.* 9:393-399. 1977) who found that trees invaded a subalpine meadow in Wyoming soon after the cessation of grazing by sheep.

It is difficult to isolate possible single causes of these tree invasions, however, by looking simply at the chronology of events. Particularly troublesome is the fact that sheepherders probably burned meadowlands in the Sierra regularly, and thus the elimination of sheep grazing involved a great reduction not only in grazing intensity but also in fire frequency. The interactions among environmental variables also detract from the attempt to find a single cause of invasion. Heavy grazing, for example, may create conditions conducive to tree invasion, but trees may not become established unless the climatic conditions are also suitable. Compounding these difficulties is the likelihood that the occasional establishment of single trees (pre-1910 or pre-1925 in Dana Meadows) is a different phenomenon (reflecting distinctive causes) from the massive establishment of trees so common in the meadows of the Sierra Nevada (after 1925 in Dana Meadows).

It is popular to suggest that forest-meadow ecotones are in "dynamic equilibrium", in that they may fluctuate with short-term changes in environmental conditions but remain stable over longer periods of time. The high frequency of young trees that are either dead or dying supports such a view for Dana Meadows. The apparent health of older trees, however, even those well within the meadow, implies that the invasion is better interpreted as a "directional" change in the vegetation.—THOMAS R. VALE, Department of Geography, University of Wisconsin, Madison 53706. (Received 7 Mar 1980; revision received 12 Sep 1980; accepted 22 Sep 1980.)